What is the evidence of contact and interaction between the two divergent lineages of Splendid Fairywren *Malurus splendens* in South Australia?

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ABSTRACT – The two distinctive subspecies of Splendid Fairywren that occur in South Australia, Black-backed *Malurus splendens melanotus* and Turquoise *M. s. callainus* Fairywrens, are not in geographical contact through the Flinders Ranges, as widely reported. Populations of the species in the northern ranges and on its eastern flank, and on its western flank in the south, vary phenotypically, some resembling Turquoise Fairywrens but many appearing intergradient. These highly variable separate populations provide the only firm evidence of hybridisation between the two subspecies. They are separated from Black-backed Fairywrens in the North Olary Plains by over 150 km east of the ranges and from others east of Orroroo in the south by about 80 km across the ranges and southern Willochra Plain. There are few records elsewhere in the Flinders Ranges. We find it likely that secondary contact and hybridisation occurred in the past, presumably during the mid to late Pleistocene, but that contact has since been lost.

INTRODUCTION

Two subspecies of Splendid Fairywren *Malurus splendens* (Quoy and Gaimard, 1832) occur in South Australia: (1) Black-backed Fairywren *M. s. melanotus* Gould, 1841 of the Murray Mallee and Olary Plains, also inland Victoria, New South Wales and southern Queensland, and (2) Turquoise Fairywren *M. s. callainus* Gould, 1867 of northern Eyre Peninsula and the north-west of the state, Central Australia and inland Western Australia. Both were long considered separate species, distinct from *Malurus splendens sensu stricto* (RAOU 1926; Condon 1968). Storr (1973) and Ford (1974a, 1974b) listed the three as conspecific and Ford (1975) described nine specimens demonstrating hybridisation between 'Splendid and Turquoise Wrens' west of the Gibson Desert in Western Australia. He speculated that contact and hybridisation might occur also between Turquoise and Black-backed Fairywrens, because of their occurrence immediately to the west and east of the Flinders Ranges respectively (Schodde 1965). Since Parker's treatment of family Maluridae in the *Interim List of Australian Songbirds* (Schodde 1975), all three have been combined consistently in one species (Schodde 1982; Rowley and Russell 1997; Schodde and Mason 1999; Higgins *et al.* 2001; Christidis and Boles 2008).

Habitats of the two subspecies are similar, dense shrublands as understorey to a variety of tall shrublands and low woodlands, including Mallee *Eucalyptus* spp., Mulga and other *Acacia* spp., *Casuarina/Allocasuarina* spp., Sugarwood *Myoporum platycarpum*, *Callitris* spp. and *Melaleuca* spp., and attributes that distinguish between the two are unclear (Higgins *et al.* 2001). Compared with its broadly allopatric congener the Purple-backed Fairywren *Malurus assimilis*, the presence of an overstorey and a more dispersed shrubland appear to favour the Splendid Fairywren, which forages more widely and is a stronger flyer (Schodde 1982; Rowley and Russell 1997).

Recent reviewers (Schodde 1982; Rowley and Russell 1997; Schodde and Mason 1999; Higgins *et al.* 2001; Kearns *et al.* 2009) have presented *callainus* and *melanotus* (subspecific names generally used hereafter for brevity) as

intergrading continuously through the Flinders Ranges. Such a putative zone of contact was examined by Reid *et al.* (1977), who reviewed distributional records for each taxon, then only recently combined in one species, and made field trips to critical localities where they took voucher specimens. They found no evidence of contact between the two subspecies, reporting a gap of about 160 km between *callainus* at Wertaloona on the eastern flank of the North Flinders Ranges and *melanotus* at Koonamore on the North Olary Plains. A narrower gap of about 80 km was identified further south, between the Port Germein district and east of Orroroo (Figure 1 shows key localities named in the text).

Reid *et al.* (1977) described and compared the plumages of ten male specimens: six *callainus*, including three from the Port Germein area that Mack (1934) had recognised as a darker subspecies *M. callainus whitei*, two recently collected *melanotus* specimens from east of Orroroo and Terowie and two from the Murray Mallee. They agreed that '*whitei*' specimens (see Discussion regarding the misuse of this name) were darker than *callainus* from elsewhere but that the crown and mantle of all were a greener blue than in *melanotus*, while specimens from east of Orroroo and Terowie fell within the range of variation of Murray Mallee *melanotus*. Schodde (1982) identified the Port Germein group as intergradient and questioned whether intergradation extended west of the Flinders Ranges, across northern Eyre Peninsula. Consequently, Schodde and Mason (1999) placed the holotype of *M. s. callainus*, taken

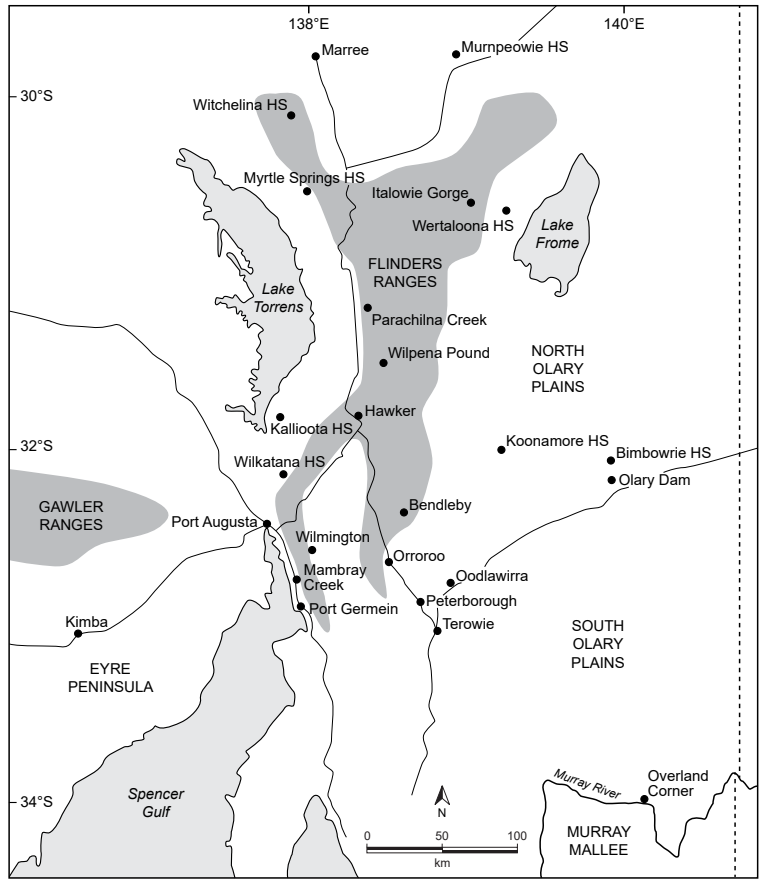

Figure 1. Map of the Flinders Ranges and adjacent regions of South Australia, showing key localities referred to in the text. Artwork Belinda Cale

immediately west of northern Spencer Gulf, in that intergradient zone; they therefore applied the name *M. s. musgravi* Mathews, 1922 to that subspecies. The holotype specimen of *Malurus callainus* Gould, 1867 in the Natural History Museum, Tring (NHMUK 1881.5.1.674) was later found to be representative of the subspecific phenotype and not intergradient when examined by R. Schodde (pers. comm.) in 2004 and by PH on 6 March 2020. The long-established name *callainus* was therefore restored and *musgravi* returned to synonymy (Schodde in Dickinson and Christidis 2014: 145; Horton *et al.* 2020; Gill *et al.* 2022).

Kearns *et al.* (2009) tested present taxonomy in a phylogeographic study of the species. They sequenced the mitochondrial gene ND2 and applied spectrophotometry to the males' coloured plumage patches whose differences in hue and shade largely define subspecies boundaries. In their genetic analysis they recovered three clades with net divergences between 1.2% and 1.4%, corresponding closely with subspecies *splendens*, *callainus* and *melanotus*. The fourth subspecies *emmottorum*, a pallid form in inland Queensland, was in the *melanotus* clade. Their limited samples from within the presumed *callainus–melanotus* hybrid zone (*sensu* Schodde and Mason 1999), one from the eastern Gawler Ranges and two from the North Flinders Ranges, were placed within the *callainus* haplogroup. Spectrophotometry was effective in recognising changes in shade between forest-occupying southern and more arid-country northern populations of *splendens* and in defining the boundary between *melanotus* and *emmottorum*. It also distinguished between subspecies *splendens*, *callainus* and *melanotus* by analysing chromatic variation of their plumage patches.

Black *et al.* (2022a) showed that the plumages of breeding males of the three subspecies *splendens*, *callainus* and *melanotus* are distinct, the hues of colour patches corresponding closely with the spectrophotometric findings of Kearns *et al.* (2009). Specimens of subspecies *callainus* are pale blue to greenish blue ('turquoise') above and have a dark violet throat and upper breast, hereafter 'bib', that contrasts with a paler blue lower breast and abdomen, hereafter 'belly', and even more strongly with the upperparts. On the other hand, the colour patches of *melanotus* specimens lie within the violet-blue to blue range and show relatively little contrast, apart from the ear patches that are paler than upperparts in all members of the species, although least obviously in *callainus*. The breast band is generally broad in *callainus* and narrow in *melanotus*, with some overlap due to the extremes of variation but with strong statistical separation; nape band widths show the same trend.

In view of the genetic divergence that Kearns *et al.* (2009) identified between *callainus* and *melanotus*, we turn to matters raised by Reid *et al.* (1977) but which remain unresolved: (1) is the Splendid Fairywren distributed continuously through the Flinders Ranges and (2) what is the nature of contact and interaction, if any, between *callainus* and *melanotus*?

We review the species' distribution in South Australia and analyse plumage variation in testing the following hypotheses concerning Flinders Ranges populations:

1. that, except for *melanotus* in the south-east, they belong to subspecies *callainus*, without intergradation, as inferred by Reid *et al*. (1977);

2. that they show continuous intergradation between *callainus* and *melanotus* as represented by Rowley and Russell (1997), Schodde and Mason (1999) and Higgins *et al.* (2001);

3. that they intergrade as a result of secondary contact between divergent lineages as hypothesised by Kearns *et al*. (2009).

METHODS

Distribution

Distributional records of the Splendid Fairywren in South Australia were collated from museum specimens, the published literature, personally obtained individual reports, and the Atlas of Living Australia (ALA https://www.ala.org.au) (including eBird records) and Birdata (https://birdata.birdlife.org.au). We closely scrutinised all records from within the Flinders Ranges by following up reports with observers where feasible and accepted those with corroborative evidence supporting correct identification.

Plumage

Plumages of all fully coloured male specimens of Splendid Fairywren in the South Australian Museum, Adelaide (SAMA) were examined by AB and PH, and those in the Natural History Museum, Tring (NHMUK) by PH. We point out here that variation in hue of the 'blue' colour patches among Splendid Fairywren subspecies extends across and beyond the nominal range of blue in the spectrum, between violet and turquoise, a greenish blue (Kearns *et al.* 2009; Black *et al.* 2022a). In total 13 variables were scored or measured:

i) dorsal patch hue, ii) bib hue, iii) belly hue, all scored visually by AB as 1 = violet, 2 = violet-blue or 3 = blue;

iv) dorsal patch shade, v) bib shade, vi) belly shade, all scored visually by AB as 1 = dark, 2 = medium or 3 = pale;

vii) dorsal patch colour, viii) bib colour, ix) belly colour, all scored visually by PH between 1 (violet) and 10 ('turquoise');

x) breast band maximum, xi) nape band maximum, the breadth of both black bands measured by AB to the nearest 0.5 mm at maximum breadth;

xii) breast band midline, xiii) nape band midline, the breadth of both black bands measured by PH to the nearest 0.5 mm within 5 mm of the midline.

The contrast in hue and shade between colour patches was noted but not scored. Two specimens in NHMUK from Wertaloona and two in the Australian National Wildlife Collection (ANWC) Canberra from Italowie, in the north-eastern Flinders Ranges, as well as additional NHMUK *callainus* specimens including the holotype, were included in the study but not analysed statistically because of incomplete data. During this phase of plumage analysis, all specimens from west of Spencer Gulf and Lake Torrens were assigned provisionally to *callainus* and all from east of the Flinders Ranges to *melanotus*. Specimens from within the Flinders Ranges and immediately adjacent were compared individually against a representative range of variation within those subspecies, as assigned.

Statistical methods

For analysis of variation among all SAMA specimens, independent of subspecific assignment, each was included in one of seven geographic samples (see Figure 2): (1) 13 western specimens from north of 28° S; (2) 8 western specimens from south of 28° S; (3) 14 eastern specimens from the Gawler Ranges and surrounds and Eyre Peninsula; (4) 8 specimens from the south-western Flinders Ranges (Kallioota Station east of southern Lake Torrens, Mambray Creek and the Port Germein area) (SW); (5) 2 specimens from the Italowie area in the north-eastern Flinders Ranges (NE); (6) 5 specimens from east and south-east of Orroroo in the south-eastern Flinders Ranges (SE); and (7) 32 specimens from the Murray Mallee and South Olary Plains.

Principal Components (PC) Analysis was used to summarise variation in scored or measured variables among SAMA specimens from the

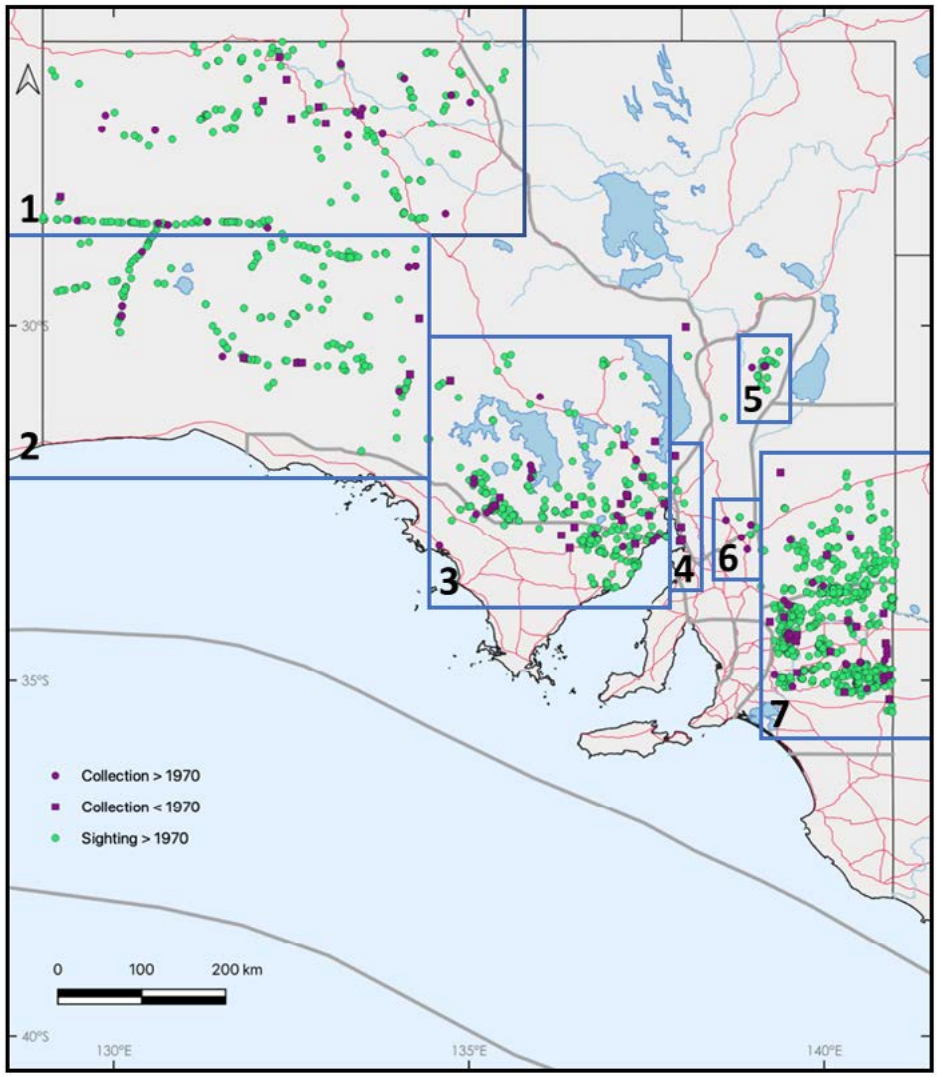

Figure 2. Distribution of Splendid Fairywren in South Australia showing records of *callainus* west of Lake Torrens and Spencer Gulf (boxes 1–3) and *melanotus* east of the Flinders Ranges (box 7). Within the Flinders Ranges there are few records except the cluster in the north-east (box 5) and those flanking the extreme south-west (box 4), and the south-east in continuity with *melanotus* (box 6). Green symbols are sight records, purple symbols are specimen records. Not all specimens examined in this study are shown on the map.

seven geographic samples, as above, and one-way Analyses of Variance and Scheffe *post hoc* tests were used to identify homogeneous groups among them, based on PC scores.

Linear Discriminant Function (DF) Analysis was then applied to samples 1–3 (*callainus*) and sample 7 (*melanotus*) as *a priori* groups to test whether they could be consistently distinguished from each other and to determine which traits best distinguished between them. Univariate comparisons were made between the two groups, using Mann–Whitney U statistic for ordinal variables and one-way analyses of variance for integral variables. DF scores from that analysis were then calculated for specimens from samples 4–6 to test whether they clustered with either of the *a priori* groups or were

separate, with DF scores intermediate between the two *a priori* groups.

All statistical analyses were performed using IBM SPSS Version 28.0 (IBM Corp, 2021).

RESULTS

Distribution

Our assessment of the distribution of Splendid Fairywren in South Australia is shown in Figure 2. Key localities are shown in Figure 1 and the latitudes and longitudes of all places named in the text are provided in the Gazetteer.

Subspecies *callainus* is broadly distributed west of Spencer Gulf and Lake Torrens, extending into Central and Western Australia, but is largely absent from the lower Lake Eyre basin (Badman 1979). Recent records on the western flank of the South Flinders Ranges include Mount Brown, and Mundallio and Wilkatana Stations (Birds SA records; P. Langdon pers. comm.). A century ago, they extended south to Mambray Creek (SAMA B3033) and the footslopes of the ranges east of Port Germein (Mellor 1913; SAMA B8405, B8406, 52790, 52802, 52803, 52820), and north to Kallioota Station between the southern tip of Lake Torrens and the ranges, where they were described as common in the scrub-covered sandhills (Morgan 1914a, 1914b; SAMA B329). Earlier records include a specimen that Frank Gibson forwarded to the SA Institute Museum from Woolundunga below Mount Brown in January 1868 and three from Marachowie immediately south of Kallioota the following year (Waterhouse 1868–1873; SA Museum archived documents). Those specimens are missing; the first was prepared as a mount for display but was probably discarded between 1882 and 1885, and a skin of the species exchanged with the Australian Museum in 1869 might account for another (Horton *et al.* 2018; AB and PH unpublished data). Within the ranges further north, a record from Parachilna Creek (Joan Paton, 4–5 birds, 16 May 1985) is supported by two subsequent observations nearby (Birdata). Beyond Parachilna are records at Myrtle Springs (Reid *et al.* 1977) and Witchelina (C. Cain, egg clutch, SAMA B22132; Birds SA surveys, Figure 3). Immediately north of the North Flinders Ranges, AB saw five birds, including a blue-winged uncoloured male, on Murnpeowie Station on 5 September 2007.

A substantial population, well documented by observations and skin specimens, is present in the northern Flinders Ranges and on its eastern flank between Nepabunna, Italowie Gorge, Balcanoona and Wertaloona. The species was not recorded elsewhere during biological surveys of the Flinders Ranges (Brandle 2001). Other reports (ALA, eBird, Birdata) from the North Flinders Ranges (9), the surroundings of Wilpena (6) and South Flinders Ranges near Melrose and Quorn (8) lacked corroborative documentation, and 11 of 13 responding reporters acknowledged errors of identification or data entry (pers. comm. to AB). Of nine eBird lists, four contained other likely errors and eight missed the locally common Purple-backed Fairywren. One observer listed both species from Wilpena Pound, identifying a Splendid Fairywren female as subspecies ‘melanotus’.

The eastern subspecies *melanotus* extends from the Victorian and South Australian Murray Mallee north through the South Olary Plains, generally to the Barrier Highway, with records beyond in Bimbowrie Conservation Park (Reid *et al.* 1977; B. Haase pers. comm.), at Olary Dam (AB 7 May 2001) and in remnant mallee between Orroroo, Peterborough and Oodlawirra (Reid *et al.* 1977; Bonnin and Rix 1980; SAMA B29320, B30406, B30407, B30408) (Figures 1 and 2). The subspecies is not generally found further north, being unrecorded from the Bendleby Range (K. Bellchambers unpublished report; AB pers. obs.) or during surveys of the North Olary Plains (Playfair and Robinson 1997), the Koonamore specimen SAMA B25354 (Schodde 1965) being an exception.

Figure 3. Male Turquoise Fairywren *Malurus splendens callainus* near Teatree Swamp, Witchelina Nature Reserve, 1 September 2014, showing typical traits of the subspecies: pale blue crown and dorsum (though lacking the turquoise seen in many individuals, perhaps as an artefact of photographic reproduction), dark violet bib and contrasting paler blue belly separated by a broad breast band. Image B. Blaylock

Plumage

Diagnostic attributes of the plumages of *callainus* and *melanotus* were published by Black *et al.* (2022a) and are provided numerically in Table 1 (see also statistical results and Discussion). Colour patch colours are described from a greenish blue ('turquoise') across the blue spectrum and into the violet range. Dorsal patch shade closely parallels colour, the palest blue of *callainus* being the most turquoise and the darkest blue of *melanotus* approaching the violet range. More variation is present in bib and belly patches but the bib in *callainus* is almost always violet and darker than the bluer belly.

Plumages of specimens from the flanks (SW and SE) and interior and eastern flank (NE) of the Flinders Ranges are summarised in Table 2 and compared with those of subspecies *callainus* and *melanotus*.

We affirm that the holotype of subspecies *callainus* lacks intergradient traits, its dorsum (scored 10) and belly (9) being among the palest and most turquoise, although its breast band midline width of 2.5 mm is towards the narrow end of the range for *callainus*.

Of six male skins known from the North Flinders Ranges only the two in SAMA were fully assessed; SAMA B32488 from 8 km south-west of Italowie Gorge is darker dorsally than all *callainus* specimens, as defined above, and its hue is intermediate between *callainus* and *melanotus*, whereas its dark bib and broad breast band are typical of *callainus*; SAMA B32489 from 3 km west of Nepabunna is slightly paler dorsally, although still darker than most *callainus*, and has a paler bib and a narrow breast band typical of *melanotus*. The two NHMUK specimens, 1965.5.56 and 1965.5.57 from near Wertaloona Homestead, are among the palest examples assigned to *callainus* by Harrison (1974: 200–201) and are confirmed as such by PH (pers. obs.), but the breast band of 1965.5.56 is of *melanotus*

Table 1. Comparison between *Malurus splendens callainus* (samples 1–3, n = 35) and *M. s. melanotus* (sample 7, n = 32) for 13 variables. Descriptive statistics are given as mean ± standard deviation (minimum–maximum). Statistic and p-values are derived from [1]Mann–Whitney U for ordinal variables or [2]one-way analyses of variance.

Variable	*callainus* n = 35	*melanotus* n = 32	Statistic	p
Dorsal patch hue	3.0 ± 0.00 (3–3)	2.4 ± 0.50 (2–3)	0.00[1]	< 0.001
Bib hue	1.0 ± 0.00 (1–1)	2.1 ± 0.23 (2–3)	0.00[1]	< 0.001
Belly hue	3.0 ± 0.00 (3–3)	2.9 ± 0.29 (2–3)	925.00[1]	0.050
Dorsal patch shade	2.97 ± 0.17 (2–3)	1.0 ± 0.00 (1–1)	0.00[1]	< 0.001
Bib shade	1.0 ± 0.00 (1–1)	1.0 ± 0.00 (1–1)	n/a	n/a
Belly shade	2.3 ± 0.45 (2–3)	2.1 ± 0.29 (2–3)	825.00[1]	0.048
Dorsal patch colour	8.5 ± 1.09 (7–10)	3.9 ± 0.70 (3–5)	0.00[1]	< 0.001
Bib colour	2.9 ± 1.28 (1–5)	4.9 ± 1.42 (3–7)	371.00[1]	< 0.001
Belly colour	6.9 ± 0.99 (4–9)	4.8 ± 1.36 (3–7)	347.00[1]	< 0.001
Breast band maximum	5.5 ± 1.30 (3.5–8.0)	3.0 ± 0.76 (1.5–5.5)	83.68[2]	< 0.001
Nape band maximum	6.2 ± 1.89 (3.0–9.0)	5.3 ± 1.06 (3.0–7.5)	5.49[2]	0.022
Breast band midline	4.0 ± 1.07 (2.0–6.0)	1.6 ± 0.67 (0.5–3.5)	91.60[2]	< 0.001
Nape band midline	5.2 ±1.73 (2.0–9.0)	4.3 ± 1.47 (1.0–9.0)	7.23[2]	0.009

width. The other two specimens, ANWC 48282 and ANWC 48283 from Italowie Gorge are dark dorsally, resembling SAMA B32488, and have narrow breast bands (estimated from photographs *per* L. Joseph).

Five specimens from Mambray Creek and the Port Germein area are darker above than all but one *callainus* specimen (SAMA B15407 from Coniston, Central Australia), while two are darker still, and the hue of all seven is mid blue and intermediate between *callainus* and *melanotus* (Figure 4); underparts vary, not all showing the typically dark violet bib of *callainus* and the belly hue in most is less contrasting (Figure 5). Breast band widths are variable but many fall between the means of each subspecies and within their overlapping range (Table 2). The Kallioota specimen SAMA B329, while typical of *callainus* in plumage colouration, has a distinctly narrow breast band. A coloured male photographed at Mundallio Station east of Port Augusta in October 1998 (Brian Furby in Collier *et al.* 2000 opposite p. 148) shows less distinction between the hues of bib, belly and dorsum than is generally found in *callainus* and it too has a narrow breast band, typical of *melanotus*.

The five specimens from east of Orroroo, Peterborough and Terowie were all judged consistent with *melanotus* in plumage, although SAMA B29321 is among the palest and bluest

Table 2. Summary findings among South Australian Museum specimens from within or near the Flinders Ranges, compared with *M. s. callainus* specimens to the west (samples 1–3) and *M. s. melanotus* specimens from the Murray Mallee (sample 7). NE, SW and SE refer to specimens in the north-east interior and flank of the ranges (sample 5), and south-west (sample 4) and south-east (sample 6) flanks of the ranges, respectively. Breast band measurements for the two main populations are mean ± standard deviation (minimum–maximum). Note that the scoring system for dorsal patch shade and colour is coarse and the numbers do not always reflect the subtle differences between specimens.

Population (sample number)	Registration number SAMA B	Dorsal patch shade and colour (scores)	Contrast dorsum with bib: hue, shade	Breast band Midline, mm	Breast band Maximum, mm	Phenotype
West of Flinders Ranges (1–3)		pale blue to greenish blue (2–3, 7–10)	strong, strong	3.96 ± 1.07 (2–6)	5.47 ± 1.30 (3.5–8)	*callainus*
NE (5)	32489	mid blue (2, 7)	strong, strong	1.5	4	intergrade
NE (5)	32488	darker blue than 32489 (2, 7)	strong, strong	3	4.5	intergrade
SW (4)	8405	as 32488 (2, 7)	strong, moderate	2	4.5	intergrade
SW (4)	8406	as 32488 (2, 7)	strong, moderate	1.5	3.5	intergrade
SW (4)	3033	as 32488 (2, 7)	strong, moderate	3.5	5.5	intergrade
SW (4)	52790, 52820	as 32488 (2, 7)	strong, moderate	3–4	4.5	intergrades
SW (4)	52802, 52803	as 32488 but slightly darker (2, 6)	strong, moderate	3–4	4.5–5	intergrades
SW (4)	329	pale blue, near greenish blue (3, 8)	strong, strong	1.5	3.5	intergrade, close to *callainus*
SE (6)	29320, 30406, 30407	dark violet-blue (1, 4)	little, none	2–2.5	2.5–3.5	*melanotus*
SE (6)	29321	dark blue, paler and less violet-blue than 29320 (1, 5)	little, none	1	2	*melanotus*
SE (6)	30408	darker violet-blue than 29320 (1, 3)	none, none	3.5	4	*melanotus*
Murray Mallee (7)		medium to dark violet-blue to blue (1, 3–5)	little or none, none	1.58 ± 0.67 (0.5–3.5)	2.95 ± 0.76 (1.5–5.5)	*melanotus*

in our sample. Breast band width is in the narrow, *melanotus* range for three specimens, but intermediate in B29320 and broad, slightly below average for *callainus*, in B30408.

Statistical results

Bib shade differed little among specimens (Figure 5) and all were scored equally (Table 1) so this variable was excluded from the multivariate analyses. Principal Components (PC) Analysis showed that 79.7% of the variation in the remaining twelve variables could be summarised by four PCs (Table 3). There were significant differences among the seven geographic samples in PC1 scores ($F_{6,75} = 63.555$, $p < 0.001$) and PC3 scores ($F_{6,75} = 3.086$, $p = 0.009$) but none for PC2 and PC4 scores ($p \geq 0.42$).

Figure 4. Dorsal view of male specimens of Splendid Fairywren from South and Central Australia: three *melanotus* from the Murray Mallee (left) showing extremes of colour variation in this subspecies, five intergradient specimens from the Flinders Ranges region (middle) and three *callainus* (right) also showing extremes of colour variation. SAMA skins left to right: (1) B19937 Sandleton; (2) B1077 Overland Corner; (3) B23281 Pungonda; (4) B32488 Italowie Gorge; (5) B52802, (6) B8406 and (7) B8405 all Port Germein; (8) B3033 Mambray Creek; (9) B15407 Coniston, Central Australia; (10) B23405 Wilcherry, Eyre Peninsula; (11) B5687 Kimba, Eyre Peninsula. Image P. Horton

Figure 5. Ventral view of male specimens of Splendid Fairywren from South and Central Australia: three *melanotus* from the Murray Mallee (left) with narrower breast bands, five intergradient specimens from the Flinders Ranges region (middle) with variable breast bands, and three *callainus* (right) with broader breast bands. Variability is limited in the appearance of the bib but is very evident in the belly. Specimen order, registration numbers and localities are the same as in Figure 4. Image P. Horton

Scheffe *post hoc* tests did not identify consistent homogeneous groups based on PC3 scores, but identified two homogeneous groups on PC1 scores, consisting of samples 1–5 ($p \geq 0.105$) and samples 6 and 7 ($p \geq 0.556$). These two groups differed significantly ($p \leq 0.0005$; Figure 6). Within the Flinders Ranges, samples 4 and 5 did not differ significantly from each other or from samples 1–3 ($p = 0.08–1.00$) although PC scores from samples 4 and 5 trend to the left margin of the combined cluster (Figure 6). Sample 6 did not differ significantly from sample 7 ($p = 0.98$).

Discriminant Function (DF) Analysis of the 12 variables using *callainus* (samples 1–3, n = 35) and *melanotus* (sample 7, n = 32) as *a priori* groups resulted in a highly significant DF (Wilk's $\lambda = 0.010$, $\chi^2 = 273.9$, $p \leq 0.0005$) which accounted for 100% of the variance and correctly identified all 67 specimens. All variables showed statistically significant differences between the *a priori* groups (Tables 1, 4). The variable 'dorsal patch shade' had the highest DF loading and correlation with the DF (0.81 cf. ≤ 0.31 for all others, Table 4), suggesting that this was the most diagnostic character separating *callainus* and *melanotus*.

From this DF, scores were calculated for the 15 Flinders Ranges specimens. All five from sample 6 (SE) were identified as *melanotus*. Seven of eight SW specimens (sample 4) and the two NE specimens (sample 5) clustered between *callainus* and *melanotus* close to the zero but on the positive (*callainus*) side, reflecting their inclusion among *callainus* in the PC analysis, as above. The eighth SW (Kallioota) specimen clustered with *callainus* and one *callainus* specimen (SAM B15407 from Coniston, Northern Territory) clustered with the Flinders Ranges group (Figure 7).

Table 3. Loadings of twelve variables, used in a Principal Components (PC) Analysis of *M. splendens,* on the four resulting PCs. Bib shade was excluded from the PC analysis because its score did not vary among specimens. * loadings <0.3

Variable	**PC1**	**PC2**	**PC3**	**PC4**
Dorsal patch hue	0.615	*	*	0.422
Bib hue	-0.877	*	*	*
Belly hue	*	*	*	0.953
Dorsal patch shade	0.882	*	0.317	*
Belly shade	*	*	0.805	*
Dorsal patch colour	0.847	*	0.423	*
Bib colour	-0.694	*	0.341	*
Belly colour	0.505	*	0.691	*
Breast band maximum	0.873	*	*	*
Nape band maximum	*	0.925	*	*
Breast band midline	0.867	*	*	*
Nape band midline	*	0.931	*	*
Variance explained (%)	**47.0**	**13.4**	**10.7**	**8.6**

Table 4. Raw (unstandardised) Discriminant Function (DF) coefficients between variables, in descending order of correlation with the resulting DF. Note that a negative figure has the same discriminant value as the equivalent positive figure. Bib shade was excluded from the DF analysis because its score did not vary among specimens.

Variable	DF coefficient	Correlation with DF
Dorsal patch shade	7.835	0.81
Dorsal patch colour	0.084	0.25
Breast band maximum	0.369	0.13
Breast band midline	0.025	0.12
Dorsal patch hue	0.522	0.09
Belly colour	0.110	0.09
Belly shade	-0.009	0.03
Nape band maximum	0.027	0.03
Nape band midline	0.067	0.03
Belly hue	0.043	0.02
Bib hue	-0.242	-0.08
Bib colour	-1.975	-0.31
constant	**-16.309**	

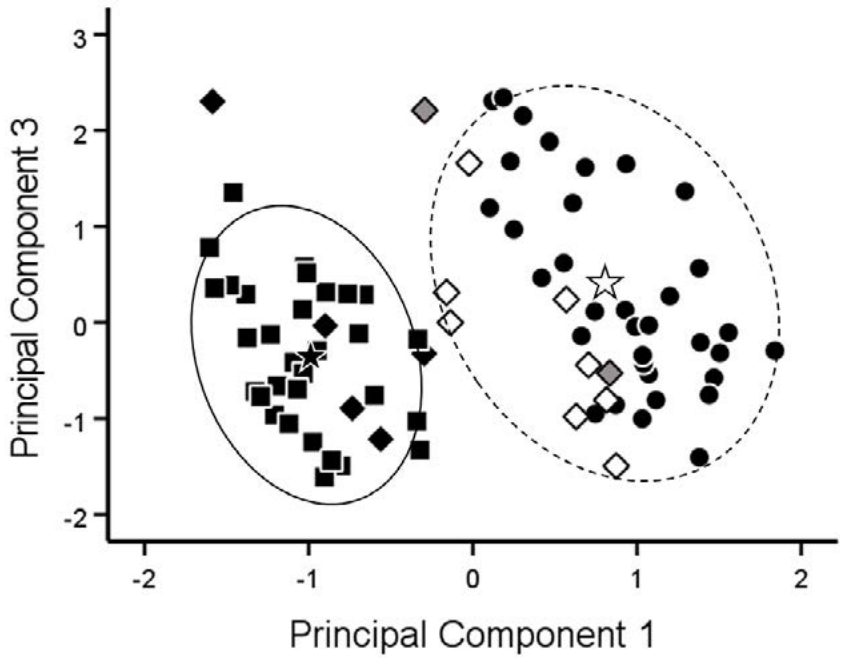

Figure 6. Scatter plot of Principal Components 1 and 3 scores for Splendid Fairywrens from west of (samples 1–3 ●), within (sample 4 ◇, sample 5 ◈, sample 6 ◆) and east of (sample 7 ■) the Flinders Ranges. The stars show the PC centroids and ovals show 95% confidence ellipses around two groups.

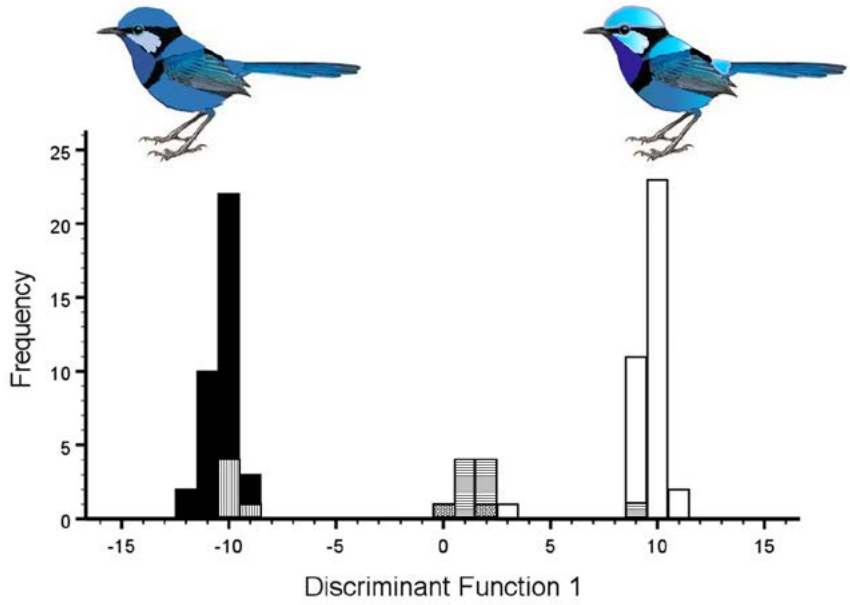

Figure 7. Histogram of Discriminant Function scores for Splendid Fairywrens based on twelve plumage variables. DF scores below zero were assigned to *melanotus* (sample 7 = black, sample 6 = vertical lines) and scores above zero to *callainus* (samples 1–3 = white, sample 4 = horizontal lines, sample 5 = stipple). Artwork characterises the distinctive phenotypes of *M. s. melanotus* (left) and *M. s. callainus* (right).

DISCUSSION

Distribution

Contrary to assumptions in recent reviews (Schodde 1982; Schodde and Mason 1999; Higgins *et al.* 2001; Kearns *et al.* 2009), we find that Splendid Fairywren distribution is disjunct across the Flinders Ranges and thus confirm the findings of Reid *et al.* (1977). In the North Flinders Ranges, apart from the population centred on Italowie Creek, the few corroborated records are on Murnpeowie, Myrtle Springs and Witchelina, and along Parachilna Creek. In the south, records immediately east of Lake Torrens and Spencer Gulf are limited to the western margins of the ranges between Kallioota in the north and Port Germein in the south. Other reports from around Wilpena, Quorn, Wilmington and Melrose have not been verified and the species is either absent from those parts of the Flinders Ranges or occurs rarely, perhaps as vagrants.

Ford (1974b) considered *callainus* to be partly nomadic, a suggestion not rejected by Kearns *et al.* (2009) whose computed lack of geographic mtDNA structure and low nucleotide diversity might alternatively be simply the consequence of population expansion. Schodde (1982) speculated that Splendid Fairywrens east of the Flinders Ranges might not be sedentary either. While we are unaware of any detailed studies of *M. s. callainus*, long-term studies of *M. s. splendens* in south-western WA (Rowley and Russell 1997) and of *M. s. melanotus* east of the Flinders Ranges (Van Bael and Pruett-Jones 2000) found that both subspecies are generally sedentary and inhabit stable territories. Of 8,603 *M. splendens* banded, the average movement recorded from 2,694 recoveries was 1 km and the maximum was 6 km (https://www.environment.gov.au/cgi-bin/biodiversity/abbbs/abbbs-search0.pl). We provide no evidence of nomadism

in either subspecies but suspect that vagrancy beyond distributional limits might explain some reports from the Flinders Ranges, as well as the Koonamore specimen and the Olary Dam observation, which was unreplicated during at least four subsequent visits to the site between 2010 and 2017 (AB pers. obs.).

Reid *et al.* (1977) deduced that *callainus* and *melanotus* had been isolated historically by the Eyrean Barrier but, since *callainus* had penetrated the Flinders Ranges, there appeared to be no geographical barrier between the two. They therefore suggested a thorough search for evidence of contact between Wertaloona and Koonamore. Paton's (1980) subsequent Parachilna Creek record provided further evidence against a barrier between Turquoise and Black-backed Fairywrens. Reid *et al.* (1977) showed that the two populations approached more closely between the western foothills of the Flinders Ranges south of Port Augusta and the mallee east of Orroroo but found no evidence of contact there; neither do we. Their map showed the distributional limit for *callainus* enclosing all of the area between Lake Torrens and the ranges. We have found only the Parachilna Creek records as firm evidence for their occurrence between Kallioota and Myrtle Springs; the distributional gap identified on the eastern flank of the ranges appears precisely as they assessed it.

It is of interest that the Purple-backed Fairywren *Malurus assimilis* has a continuous west to east distribution through the Flinders Ranges, between subspecies *M. a. mastersi* and *M. a. assimilis*. The genetic divergence (1.1–1.2%) between subspecies *mastersi* and *assimilis* (McLean *et al.* 2017) is close to the 1.4% separating *callainus* and *melanotus* (Kearns *et al.* 2009).

Plumage

Despite considerable variation in many of the plumage characters within both subspecies and some overlap between them, particularly in belly patch colour (Figure 5), statistical analysis of all plumage data in this study amply confirms the diagnostic separation of subspecies *callainus* and *melanotus* (Table 1, Figures 6 and 7).

A notably dark specimen of *callainus* (with the most violet bib and least turquoise dorsum) from Coniston (B15407, Figures 4 and 5) among a limited Central Australian sample brought to mind Harrison's (1974: 201) report of 'a distinct clinal increase in the depth of colour of the breast and belly [= belly in this study] from a paler blue on the eastern side of the [Flinders] range near Lake Frome, to a deep blue near Warburton [WA] in the west'. He also reported 'a similar but less striking increase in the depth of colour on the throat' [= bib] but did not note any trend in dorsal colour. Although we noted a slight increase in mean belly colour score from sample 3 north-westwards to sample 1, we detected no significant geographical trend in other plumage variables and so failed to support Harrison's inference which was evidently based on an examination of as few as 17 coloured males taken during the Harold Hall Australian Expeditions. Furthermore, our three geographic samples of *callainus* clustered consistently, and evidence of intergradation was detected only within Flinders Ranges samples 4 and 5 that Reid *et al.* (1977) had included among *callainus*.

Despite incomplete data for the six NE Flinders Ranges skins, we find that their dorsal plumages vary from matching the palest of *callainus* (the two NHMUK Hall Expedition specimens) to exceeding the darkest (including the two ANWC specimens), thus approaching that of *melanotus*; breast band widths, measured or estimated, are also variable but appear mostly to fall between the means of both subspecies (Table 2).

Reid *et al.* (1977) found that three SW Flinders specimens that Mack (1934) had identified as subspecies *whitei* (see below) were darker than other *callainus*, providing possible evidence of hybridisation, but inferred rather that they were

an isolated population of *callainus* under the selective influence of a more humid environment along the western scarp of the southern Flinders Ranges. We find that the specimens that they examined and four others from the Port Germein area in the S. A. White Collection in SAMA are 'close to a perfect intermediate of the two' (Schodde 1982: 56). Their breast bands are variable and many are in the overlap range and between the means of the two subspecies (Table 2), while the Kallioota and Mundallio birds have narrow breast bands of *melanotus*-width.

SE specimens from east of Orroroo, Peterborough and Terowie are consistent with the *melanotus* phenotype although recognition of intergradient traits among them might be precluded by the limited sample size, with one specimen among the palest and another with a breast band among the broadest.

Interaction in the Flinders Ranges

Our first hypothesis, that SW and NE Flinders birds (samples 4 and 5) belong to subspecies *callainus*, is not rejected by all statistical analyses, the PC scatterplot showing them clustered with *callainus*, although mostly placed towards the *melanotus* cluster (Figure 6). On the other hand, the DF histogram places all but the Kallioota specimen in an intermediate position between the two subspecies albeit on the *callainus* side of zero (Figure 7). While the SW sample's darker phenotype might result from climatic influences of reduced temperature and aridity on an isolate of *callainus*, as argued by Reid *et al.* (1977), we find a phenotypic intergradient explanation more plausible. Furthermore, the variable but mostly intermediate breast band width present in that sample seems an unlikely character to respond to such selection. More pronounced variation occurs among the NE population, as observed by Schodde (1982), where the plumages of some specimens are as dark as in the SW, while others resemble the palest within *callainus*. Support for our first hypothesis is therefore qualified and limited.

Our second hypothesis, that the two taxa are in contact through an intergradient zone, is rejected by the recognition of two distinct groupings in the PCA and by their discontinuous distribution.

Our third hypothesis of hybridisation between the two subspecies, despite their present allopatry, is supported by the variation within both NE and SW samples and in the statistical analyses. Moreover, while the NHMUK and Kallioota specimens closely resemble the *callainus* phenotype, almost all representatives of these two populations show intermediate plumage traits of colour patch hue and/or breast band width. Such hybridisation would have resulted from past contact across the Eyrean Barrier through the Flinders Ranges. The NE and SW Flinders Ranges populations might both be considered small hybrid swarms (see below).

The evidence of intergradation present in the SW population (sample 4) suggests earlier reproductive contact with the SE population (sample 6) across the southern Willochra Plain between Wilmington, Booleroo Centre, Orroroo and Peterborough. While this appears plausible, much of the plain's natural cover immediately preceding its development for pasture and cereal production consisted of Irongrass *Lomandra* Tussock Grassland (Specht 1972). Because mallee scrub was evidently greatly restricted across the plain, there might have been little or no suitable habitat then for the species across this potential zone of interaction. Limited information about historical bird distribution in this area from Gray (1931, 1932, 1933) and Brandon (1936, 1948) included lists of birds identified from the vicinity of Orroroo and Wilmington respectively. Both recorded White-winged *Malurus leucopterus* and Purple-backed *M. assimilis* Fairywrens but neither Turquoise nor Black-backed Fairywren.

Absence of the species between Wertaloona and Koonamore is probably also explained by the lack of suitable habitat for the species. An almost corresponding gap between subspecies of Thick-billed Grasswren *Amytornis modestus*

was attributed to the relatively limited extent of shrubland between the range and Lake Frome (Black *et al.* 2011).

Mathews (1912) described the SW population from the Port Germein area as *Malurus melanotus germaini*. Earlier, Campbell (1902) had named specimens from 'the interior' (of New South Wales, not South Australia) as *M. whitei* but later, Mathews (1922) mistakenly gave the names *whitei* and *germaini* as synonyms and the error was not corrected until Schodde (1982), who included *germaini* in *callainus* and *whitei* in *melanotus*.

Hybrid swarms

The concept of the hybrid swarm (Anderson 1949; Short 1969) is of hybrid populations existing largely or entirely independently of populations of one or both parental taxa. Their development can follow anthropogenic habitat and other changes (Hasselman *et al*. 2014; Freed *et al.* 2015; Wells *et al.* 2019) or occur naturally in an evolutionary context, potentially giving rise to hybrid species (Seehausen 2004; Masello *et al*. 2019). Australian examples of hybrid swarms include those involving non-sister thornbill *Acanthiza* species (Black *et al.* 2015), genetically divergent subspecies of Australian Ringneck *Barnardius zonarius* (Joseph and Wilke 2006) and Copperback Quailthrush *Cinclosoma clarum* (Black *et al.* 2019), and genetically close subspecies of Crimson Rosella *Platycercus elegans* (Black *et al.* 2022b).

Of two hybrid swarms identified here, the northern population is a typical example, distant from parental *melanotus* by over 150 km, and only loosely associated with *callainus* through small isolates or possible vagrants such as those identified on Murnpeowie and Witchelina. Also typically, it consists of highly variable individuals covering a phenotypic range between parental forms. The southern '*germaini*' group is less distantly isolated from *melanotus*, and its association with *callainus* is also closer but tenuous nonetheless, separated from Myall *Acacia papyrocarpa* woodland to the west by about 20 km of sparsely vegetated flats and salinas between Lake Torrens and the northern tidal reaches of Spencer Gulf. While its plumages are more consistent among the seven '*germaini*' specimens, there is variation in that population also, that is especially evident from inclusion of the Kallioota and Mundallio examples.

Biogeography and taxonomic rank

Kearns *et al.* (2009) inferred that subspecies *callainus* (as *musgravi*) and *melanotus* diverged in allopatry across the biogeographic Eyrean Barrier during the Pleistocene but are continuously distributed through the Flinders Ranges. We find on the contrary that the subspecies are allopatric and that the species' presence within the Flinders Ranges is limited to one small hybrid population and a few isolated records, with a second hybrid population on the SW flank and one *melanotus*-like population on the SE flank. Our findings support the hypothesis that separation and divergence of *callainus* and *melanotus* in allopatry have been followed by expansion, secondary contact and hybridisation. However, there is no existing hybrid zone and only remnant populations of hybrid phenotype persist, principally as hybrid swarms, showing that secondary contact has been lost.

Because conditions have ameliorated since the extreme aridity of the last glacial maximum (LGM) c. 18,000 years ago, the two divergent lineages might not have been in contiguous distribution at any time during this period, making it likely that contact was lost at LGM or earlier. Kearns *et al.* (2009) inferred a population expansion in both subspecies, sufficient to allow secondary contact and hybridisation. This could have taken place during an inter-glacial pluvial period of the Pleistocene before LGM.

Turquoise and Black-backed Fairywrens show a degree of phenotypic and genetic distinction

that attests to a prolonged period of independent evolution. Hybridisation between the two has occurred in the past but to a limited extent. The process of speciation was incomplete at the point of secondary contact, but the two lineages now appear to be allopatric and, if gene flow has ceased, speciation may continue. Such taxa are recognised as semispecies or allospecies (Short 1969; Ford 1987; Winker 2021) or as evolutionarily significant units (ESUs) (Moritz 1994; Fraser and Bernatchez 2001); their reproductive isolation is moot but gene flow is likely at least to be restricted. Under the biological species concept, they fall into Winker's (2021) 'Gray Zone' of 'almost-species' but are treated taxonomically as subspecies on the basis of present evidence.

Limitations to the study

Given the phenotypic similarities of subspecies of Splendid Fairywren and the variation present within them, sample size will limit the resolving power of statistical analysis. Our samples from within the critical Flinders Ranges region were necessarily small, many specimens were very old, and not all were included in the full analysis. Yet the use of museum specimens allows a degree of objectivity not necessarily achieved with field-based research, because of difficulties in the interpretation of colour in naturally variable lighting conditions, or with photographic studies unless closely standardised methods are employed. We anticipate the need for further research into the interaction between subspecies *callainus* and *melanotus* and between *splendens* and *callainus*, including genome-level analysis of adequate samples across the species' distribution.

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Gazetteer of localities named in the text. Those given in **bold** are shown on the map (Figure 1). HS = homestead.

Locality	Latitude, Longitude
Balcanoona HS	30° 32′ S, 139° 18′ E
Bendleby	**32° 31′ S, 138° 47′ E**
Bimbowrie HS	**32° 03′ S, 140° 09′ E**
Booleroo Centre	32° 53′ S, 138° 21′ E
Coniston	22° 03′ S, 132° 30′ E
Italowie Gorge	**30° 31′ S, 139° 12′ E**
Kallioota HS	**31° 50′ S, 137° 55′ E**
Koonamore HS	**32° 03′ S, 139° 23′ E**
Kimba	**33° 08′ S, 136° 28′ E**
Mambray Creek	**32° 50′ S, 137° 59′ E**
Marachowie HS	31° 59′ S, 138° 03′ E
Melrose	32° 50′ S, 138° 11′ E
Mount Brown	32° 30′ S, 138° 00′ E
Mundallio HS	32° 28′ S, 137° 53′ E
Murnpeowie HS	**29° 35′ S, 139° 03′ E**
Myrtle Springs HS	**30° 27′ S, 138° 13′ E**
Nepabunna	30° 35′ S, 138° 59′ E
Olary Dam	**32° 13′ S, 140° 18′ E**
Oodlawirra	**32° 53′ S, 139° 04′ E**
Orroroo	**32° 44′ S, 138° 37′ E**
Overland Corner	**34° 09′ S, 140° 20′ E**
Parachilna Creek	**31° 11′ S, 138° 28′ E**
Peterborough	**32° 59′ S, 138° 50′ E**
Port Augusta	**32° 30′ S, 137° 47′ E**
Port Germein	**33° 01′ S, 138° 00′ E**
Pungonda	34° 28′ S, 140° 52′ E
Quorn	32° 31′ S, 138° 03′ E
Sandleton	34° 28′ S, 139° 21′ E
Terowie	**33° 09′ S, 138° 55′ E**
Warburton	26° 08′ S, 126° 35′ E
Wertaloona HS	**30° 38′ S, 139° 21′ E**
Wilcherry	32° 50′ S, 136° 30′ E
Wilkatana HS	**32° 10′ S, 137° 54′ E**
Willochra Plain, southern	32° 40–55′ S, 138° 10–30′ E
Wilmington	**32° 39′ S, 138° 06′ E**
Wilpena Pound	**31° 33′ S, 138° 34′ E**
Witchelina HS	**30° 01′ S, 138° 03′ E**
Woolundunga	32° 32′ S, 137° 57′ E